

On the diversity of the SE Indo-Pacific species of *Terebellides* (Annelida; Trichobranchidae), with the description of a new species

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ABSTRACT

The study of material collected during routine monitoring surveys dealing with oil extraction and aquaculture in waters off Myanmar (North Andaman Sea) and in the Gulf of Thailand, respectively, allowed us to analyse the taxonomy and diversity of the polychaete genus *Terebellides* (Annelida). Three species were found, namely *Terebellides* cf. *woolawa*, *Terebellides hutchingsae* **spec. nov.** (a new species fully described and illustrated), and *Terebellides* sp. (likely a new species, but with only one available specimen). The new species is characterised by the combination of some branchial (number, fusion and relative length of lobes and papillation of lamellae), and thoracic (lateral lobes and relative length of notopodia) characters and is compared with all species described or reported in the SW Indo-Pacific area, as well as with those sharing similar morphological characteristics all around the world. The taxonomic relevance of the relative length of branchial lobes and different types of ciliature in branchial lamellae for species discrimination in the genus is discussed. A key to all *Terebellides* species described in SE Indo-Pacific waters is presented.

Subjects Biodiversity, Marine Biology, Taxonomy, Zoology

Keywords Polychaeta, *Terebellides*, New species, Branchial morphology, SEM, Thailand, Myanmar

INTRODUCTION

The genus *Terebellides* is characterised by a combination of several characters including the compact appearance of the prostomium, a peristomium forming two lips (upper and lower), a thorax composed by 18 chaetigers, capillary notochaetae, denticulate thoracic neurochaetal hooks and abdominal avicular uncini. Nevertheless, the two most distinctive characters are the single mid-dorsal branchiae composed by 2–5 lamellate lobes, and the geniculate chaetae present in the first 1–2 thoracic neuropodia (*Schüller & Hutchings, 2013*).

The peculiar shape of the branchiae of the type species (i.e., *T. stroemii* *Sars, 1835*) was one of the main facts that led to attributing most of the subsequent records to this taxon, especially in the 19th century and most part of the 20th, when only a few characters were enough to discriminate the different species. Therefore, the number of fully described species was relatively low and *T. stroemii* was thought as being cosmopolitan.

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The ‘Catalogue of World Polychaetes’ by [Hartman \(1959\)](#) contributed to this consideration by synonymizing several species with *T. stroemii* (e.g., *T. ypsilon*). As a result of this, up to 1980s this species was reported from a wide variety of world areas and depths. However, in the late 20th century, this set of characters was gradually revealed not to be enough to distinguish among species. The study done by [Williams \(1984\)](#) clearly showed that a new set of characters was needed to differentiate species. [Imajima & Williams \(1985\)](#) and [Solis-Weiss, Fauchald & Blankestein \(1991\)](#) further supported this trend and, thus, a progressively higher number of new species have been described (e.g., [Bremec & Elías, 1999](#); [Hilbig, 2000](#); [Hutchings & Peart, 2000](#); [Garraffoni & Lana, 2003](#); [Hutchings, Nogueira & Carrerette, 2015](#); [Parapar & Moreira, 2008](#); [Parapar, Moreira & Helgason, 2011](#); [Parapar, Mikac & Fiege, 2013](#); [Parapar, Moreira & O’Reilly, 2016](#); [Parapar et al., 2016](#); [Schüller & Hutchings, 2010](#); [Schüller & Hutchings, 2012](#); [Schüller & Hutchings, 2013](#)). At the same time new characters for the species discrimination have been reported, and those traditionally used (e.g., branchial shape) have increasingly been described in greater detail. As a result, the true diversity of the genus *Terebellides* begins to be revealed.

In the SW Indo-Pacific, ten species of *Terebellides* have been described: four from the Philippine and China Seas ([Salazar-Vallejo et al., 2014](#)), namely *T. intoshi* [Caullery, 1915](#), *T. jorgeni* [Hutchings, 2007](#), *T. sieboldi* [Kinberg, 1866](#) and *T. ypsilon* [Grube, 1878](#), and six from the Australian coasts: *T. akares* [Hutchings, Nogueira & Carrerette, 2015, *T. jitu* \[Schüller & Hutchings, 2010\]\(#\), *T. kowinka* \[Hutchings & Peart, 2000\]\(#\), *T. mundora* \[Hutchings & Peart, 2000\]\(#\), *T. narribri* \[Hutchings & Peart, 2000\]\(#\) and *T. woolawa* \[Hutchings & Peart, 2000\]\(#\). Additional references to the presence of *T. stroemii* in these waters are found in \[Caullery \\(1944\\)\]\(#\), \[Rullier \\(1965\\)\]\(#\), \[Gallardo \\(1967\\)\]\(#\), \[Stephenson, Williams & Lance \\(1970\\)\]\(#\), \[Stephenson, Williams & Cook \\(1974\\)\]\(#\), \[Gibbs \\(1971\\)\]\(#\), \[Knox & Cameron \\(1971\\)\]\(#\), \[Hutchings \\(1977\\)\]\(#\), \[Shin \\(1982\\)\]\(#\), \[Amoureux \\(1984\\)\]\(#\), \[Hutchings & Murray \\(1984\\)\]\(#\), \[Hutchings et al. \\(1993\\)\]\(#\) and \[Tan & Chou \\(1993\\)\]\(#\). In Australia and New Zealand, reports of *T. stroemii* were summarized by \[Day & Hutchings \\(1979\\)\]\(#\). Later, \[Hutchings & Peart \\(2000\\)\]\(#\) reviewed the Australian *Terebellides* and described four new species. Moreover, these authors also reviewed materials collected in the vicinity of the type locality in the SW coast of Norway and concluded that *T. stroemii* is not present in southern latitudes. Further papers by \[Hutchings \\(2007\\)\]\(#\), \[Schüller & Hutchings \\(2010\\)\]\(#\) and \[Hutchings, Nogueira & Carrerette \\(2015\\)\]\(#\) continued with the reassessment of the diversity of *Terebellides* in Australian-Indonesian coasts.](#)

Our paper addresses the study of the genus in waters off Myanmar and Thailand, allowing us to describe a new species. We are also reviewing and updating the previous works reporting this genus in the area, and we present a key to all species recorded in the SE Indo-Pacific. Our study represents one additional contribution to unveil the hidden diversity of the genus *Terebellides* in the world oceans and confirms that *T. stroemii* appears to be absent in the Indo-Pacific. Furthermore, we provide evidence supporting that the diversity of *Terebellides* is still far from being well known. This seems to be particularly true for the Indo-Pacific region as, in addition to the new one, we are also describing two more species. Despite that its particular situation (either in terms of morphology or number of available specimens) does not allow us to fully identify them, they are certainly different, thus contributing to the overall diversity of the genus in the region.

Table 1 Main abiotic characteristics: silt and organic carbon contents. Main abiotic characteristics of the samples where *Terebellides* specimens were collected. Org. car., organic carbon content (%).

	Station	Date	Longitude N	Latitude E	Depth (m)	≤ 63 μm%	Org. car.
Myanmar (N Andaman Sea)	E7	03/12/03	15°07'59.8"	94°46'46.5"	46.0	76.3	1.26
	E8	"	15°06'27.7"	94°46'50.2"	47.0	78.7	1.29
	E11	"	15°07'23.2"	94°46'45.9"	47.0	83.6	1.21
	E14	"	15°07'20.0"	94°46'51.1"	47.4	76.7	1.12
	E15	"	15°07'15.9"	94°46'51.1"	47.0	80.4	1.16
	E16	"	15°07'07.8"	94°46'51.0"	47.6	73.8	1.15
	E17	"	15°07'14.9"	94°45'25.9"	48.0	74.0	1.28
	S2	"	15°02'03.3"	94°45'45.7"	51.0	72.8	0.86
	S3	"	15°02'19.4"	94°46'02.6"	51.0	80.5	0.98
	S4	"	15°03'08.2"	94°46'03.0"	51.0	90.2	0.92
	WP2	"	15°09'06.6"	94°45'26.7"	45.5	86.2	1.19
	WP3	"	15°02'03.0"	94°46'19.2"	51.0	69.6	2.42
Gulf of Thailand	2	17/07/98	07°27'43.6"	102°39'00.1"	61.0	88.3	0.81
	3	"	07°29'20.2"	102°43'49.7"	61.0	73.6	0.74
	5	"	07°36'01.1"	102°50'32.6"	64.0	92.2	1.15
	6	"	07°40'08.9"	102°51'14.6"	66.0	95.4	1.23
	7	"	07°34'00.8"	102°45'37.2"	64.0	89.3	0.98
	8	"	07°35'23.6"	102°44'12.3"	66.0	92.7	1.20
	15	"	07°44'21.5"	102°34'58.5"	75.0	93.8	1.42
	16	"	07°43'18.8"	102°28'39.1"	77.0	90.7	1.22
	23	"	08°01'12.7"	102°18'40.2"	78.0	75.6	1.08

MATERIAL AND METHODS

This study is based on 85 specimens of the genus *Terebellides* from 26 samples collected in 21 stations during routine monitoring surveys dealing with oil extraction and aquaculture in waters off Myanmar (North Andaman Sea) in 2003 and Gulf of Thailand in 1998, respectively (Table 1).

The samples were collected by means of a van Veen grab covering about 0.3 m². The grab contents were mixed in a sufficiently large container, and then sieved out on board by pouring the contents through a 1 mm mesh sieve. The retained sediment was then transferred into a plastic bag, fixed with a 10% formaldehyde/seawater solution, stained with “Rose of Bengal” and stored until sorted. An initial sorting was performed under a dissecting stereomicroscope (Zeiss Stemi 2000-C) and the specimens of *Terebellides* were counted and preserved in 70% ethanol.

One-liter volume of sediment from one grab was used for physico-chemical analyses (viz. granulometry, organic carbon content). The sediment was taken at each station and transferred to wide-mouthed double-closing 500 ml polyethylene flasks, which were stored in the dark until transferred to the laboratory. Laser granulometry (% volume) was performed on dry sediment after sifting through a 0.8 mm mesh sieve using a Malvern Mastersizer S laser granulometer. Sediments were characterized by the percentage of silt

and clay (diameter <63 µm). Estimates of organic carbon have been made according to the European experimental standard NF ISO 14235 (oxidation method, 0.1% m/m).

Light microscope images were obtained by means of an Olympus SZX12 stereomicroscope equipped with an Olympus C-5050 digital camera. Line drawings were made by means of an Olympus BX40 stereomicroscope equipped with camera lucida. Specimens used for examination with Scanning Electron Microscope (SEM) were prepared by critical point drying, covered with gold and examined and photographed under a JEOL JSM-6400 electron microscope at the Servicios de Apoyo á Investigación-SAI (Universidade da Coruña-UDC, Spain).

Most of the obtained material was deposited in the Museo Nacional de Ciencias Naturales (Madrid, Spain; MNCN). Additional paratypes of *T. hutchingsae* **spec. nov.** were deposited in the collections of the Australian Museum (Sydney, Australia; AM) and Göteborgs Naturhistoriska Museum (Göteborg, Sweden; GNM). Type material of *Terebellides gracilis* [Malm, 1874](#) was loaned for study from the Göteborgs Naturhistoriska Museum (Holotype, GNM Polych 641). Type material of *Terebellides sieboldi* [Kinberg, 1866](#) was requested to the Swedish Museum of Natural History for comparison but only one specimen, and badly preserved, could be located (L Gustavsson, *in litt.*).

Methyl green staining pattern was determined based on the classification proposed by [Schüller & Hutchings \(2010\)](#).

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RESULTS

Systematic account

Family Trichobranchidae [Malmgren, 1866](#)

Genus *Terebellides* [Sars, 1835](#), emended by [Schüller & Hutchings, 2013](#)

Type species: *Terebellides stroemii* [Sars, 1835](#)

Terebellides hutchingsae **spec. nov.**

LSID: 78E96984-41E7-43E6-8E5D-03E9421BE306

([Figs. 1– 8](#) and [Table 2](#))

Table 2 Comparison of *Terebellides* with ciliated papillae in branchial lamellae. Comparison of several body characters of the species of *Terebellides* described with ciliated papillae in branchial lamellae.

Source	GP	LL	Branchiae				CH1	CHG	NRTU	NACH	Distribution	
			Lobes	Relative length	LCP/WDCP	PPP						
<i>T. gracilis</i> <i>Malm, 1874</i>	<i>Parapar, Moreira & Helgason (2011)^a</i>	TC4–5	TC1–5 ^b	4 ^c	Same	LCP	NO	Shorter	6	2 ^d	44	Iceland
	<i>Parapar, Mikac & Fiege (2013)</i>	TC4–5	TC1–6	4	Ventral shorter	LCP	Yes, in lower lobes	Shorter	6	2–4	30–32	Adriatic Sea
<i>T. jorgeni</i> <i>Hutchings, 2007</i>	<i>Hutchings (2007)</i>	TC 2–3 ^e	SG1–5 and SG7–8	4	Ventral shorter	WDCP ^f	No ^g	Shorter ^h	6	4–6	~48	Bali ⁱ
<i>T. mediterranea</i> <i>Parapar, Mikac & Fiege, 2013</i>	<i>Parapar, Mikac & Fiege (2013)</i>	TC4–5	TC1–5	5	Ventral much shorter	LCP	Yes	Longer	6	3–4	32	Adriatic Sea
<i>T. akares</i> <i>Hutchings, Nogueira & Carreterre, 2015</i>	<i>Hutchings, Nogueira & Carreterre (2015)</i>	TC4–5	TC1–8	5	Ventral shorter	WDCP	No ^g	Shorter	5–6	4 ^g	17–25	North-east Australia
<i>T. shetlandica</i> <i>Parapar, Moreira & O'Reilly, 2016</i>	<i>Parapar, Moreira & O'Reilly (2016)</i>	TC4–5	TC1–6	5	Ventral shorter	WDCP	Short	Shorter	6	4	27–36	Shetland Islands
<i>T. persiae</i> <i>Parapar et al., 2016</i>	<i>Parapar et al. (2016)</i>	TC4–5	TC1–6	5	Ventral shorter	WDCP	Short	Shorter	6	2–4	27–36	Iran
<i>T. hutchingsae</i> spec. nov.	This work	TC4–5	TC1–5	5	Ventral shorter	WDCP	Short	Shorter	6	4	27–30	Thailand and Myanmar

Notes.

^aFrom a redescription of Malm's holotype.

^bVery low lappets.

^cThe fifth lobe is very low and therefore branchiae could be described as with only four lobes.

^dCharacter observed from the study of several specimens under the SEM; it cannot be properly observed in holotype.

^eAuthor mentions SG3–5; this can be interpreted as NO in SG3 (TC1) and GO in SG4–5 (TC2–3); author probably meant TC3–5.

^fAuthor simply mentions “surface of (branchial) lamellae weakly papillate”.

^gNot explicitly mentioned in the original description of the species; taken from figures.

^hCH2 also smaller than subsequent ones.

ⁱThis species shows a disjunct distribution, being originally described from Bali but also reported from W and S Africa and Tasman Sea.

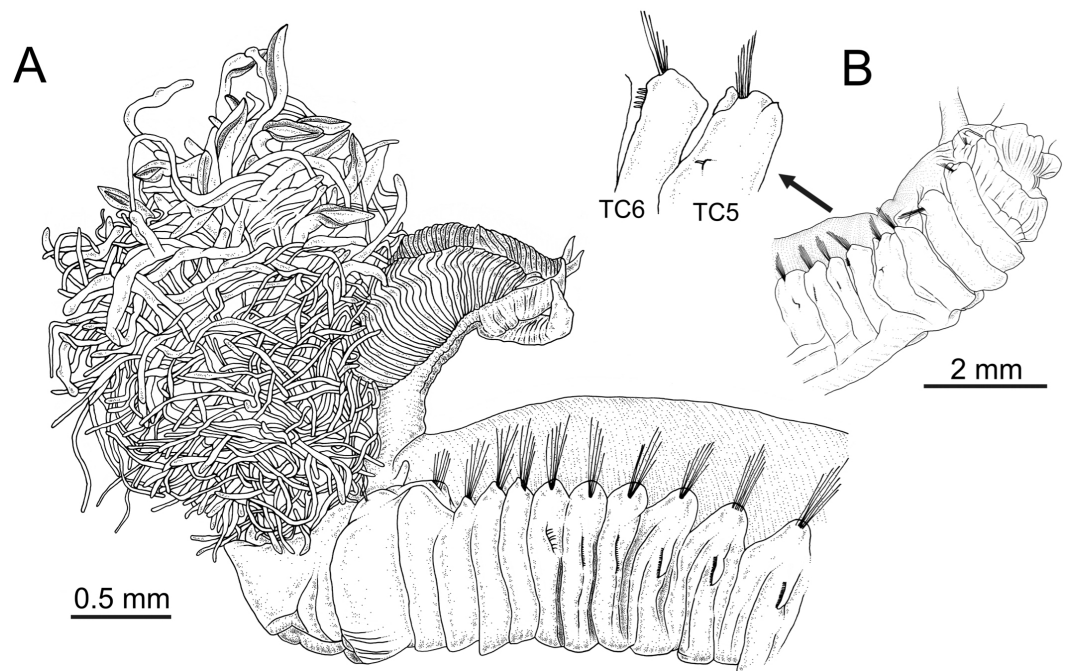


Figure 1 Line drawings of the species of *Terebellides*. *Terebellides hutchingsae* spec. nov., Holotype, MNCN 16.01/17428. (A) anterior end, left lateral view. *Terebellides* sp., MNCN 16.01/17457; (B) detail of position of geniculate chaetae in thoracic chaetiger 5 (TC5) and thoracic chaetiger 6 (TC6) of anterior right side of body.

Material examined

THAILAND (Gulf of Thailand): **Holotype**: MNCN 16.01/17428 (St. 6). **Paratypes**: MNCN 16.01/17429 (St. 2, 4 specs); MNCN 16.01/17430 (St. 3, 3 specs); MNCN 16.01/17431 (St. 5, 3 specs); MNCN 16.01/17432 (St. 5, 1 spec. on SEM stub); MNCN 16.01/17433 (St. 6, 5 specs); MNCN 16.01/17434 (St. 7, 5 specs); MNCN 16.01/17435 (St. 8, 7 specs); MNCN 16.01/17436 (St. 8, 1 spec. on SEM stub); MNCN 16.01/17437 (St. 15, 2 specs); MNCN 16.01/17438 (St. 16, 6 specs); MNCN 16.01/17439 (St. 23, 1 spec. on SEM stub). **MYANMAR** (North Andaman Sea): **Paratypes**: MNCN 16.01/17440 (St. E7(2), 1 spec.); MNCN 16.01/17441 (St. E8(3), 1 spec.); MNCN 16.01/17442 (St. E11B(2), 4 specs); MNCN 16.01/17443 (St. E11B(3), 2 specs); MNCN 16.01/17444 (St. E14(2), 4 specs); MNCN 16.01/17445 (St. E15(2), 10 specs); MNCN 16.01/17446 (St. E16(1), 2 specs); MNCN 16.01/17447 (St. E16(3), 1 spec.); MNCN 16.01/17448 (St. 17(3), 1 spec.); MNCN 16.01/17449 (St. S2(2), 1 spec.); MNCN 16.01/17450 (St. S3(2), 4 specs); MNCN 16.01/17451 (St. S3(2), 1 spec. on SEM stub); MNCN 16.01/17452 (St. S3(3), 4 specs); MNCN 16.01/17453 (St. S4(2), 2 specs); GNM Polychaeta 14880 (St. S4(3), 1 spec.); GNM Polychaeta 14881 (St. WP2(2), 2 specs); AM 48834 (St. WP2(3), 2 specs); MNCN 16.01/17454 (St. WP2(3), 2 specs on SEM stub); AM 48835 (St. WP3(3), 1 spec.).

Description (based on holotype and paratypes) Complete individuals ranging from 9.0 to 14.0 mm in length (14 mm in holotype; Figs. 1A and 2A–2B) and 0.7 to 1.5 mm in maximum width at thoracic region (1.3 mm in holotype, excluding parapodia). Body

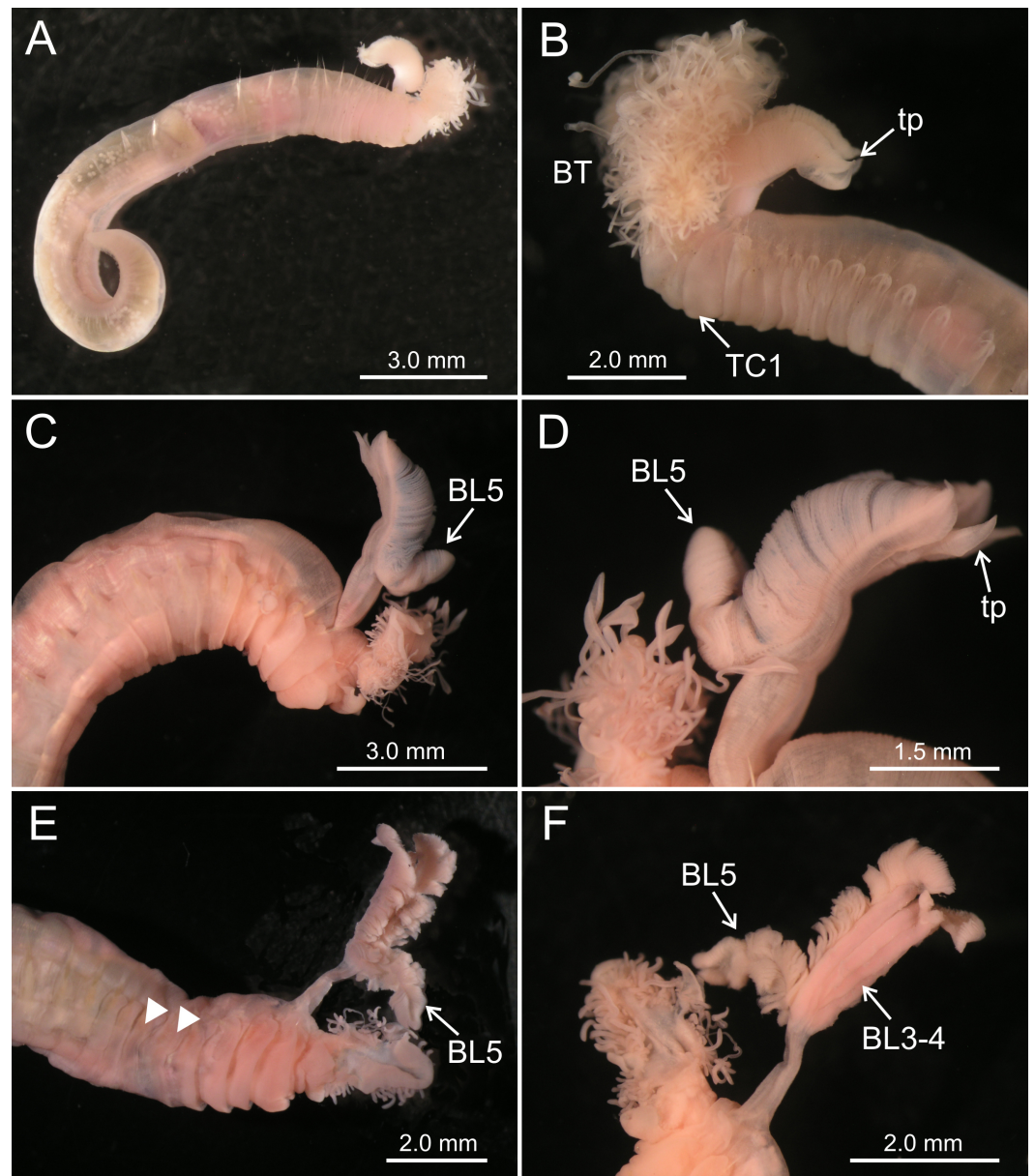


Figure 2 Stereomicroscope images of *Terebellides* spp. (A–B) *Terebellides hutchingsae* spec. nov. Stereomicroscope images. Holotype MNCN 16.01/17428; (A) general view; (B) anterior end, left lateral view. (C–D) *Terebellides* cf. *woolawa* MNCN 16.01/17455; (C) anterior end right lateral view; (D) detail of branchiae, left lateral view. (E–F) *Terebellides* sp. MNCN 16.01/17457; (E) anterior end right ventro-lateral view, arrowheads pointing to thoracic chaetiger 5 and thoracic chaetiger 6; (F) detail of branchiae in ventral view. Abbreviations: BL, branchial lobes; BT, buccal tentacles; TC, thoracic chaetiger; tp, terminal projection.

tapering posteriorly with segments increasingly shorter and crowded towards pygidium. Prostomium compact; peristomium forming a tentacular membrane with large upper and lower lips surrounding mouth, sometimes almost devoid of buccal tentacles (Fig. 3A). Buccal tentacles of two types, short ventral tentacles uniformly cylindrical or slightly expanded at tips, and long dorsal tentacles more expanded at tips (Figs. 2B and 4A–4B).

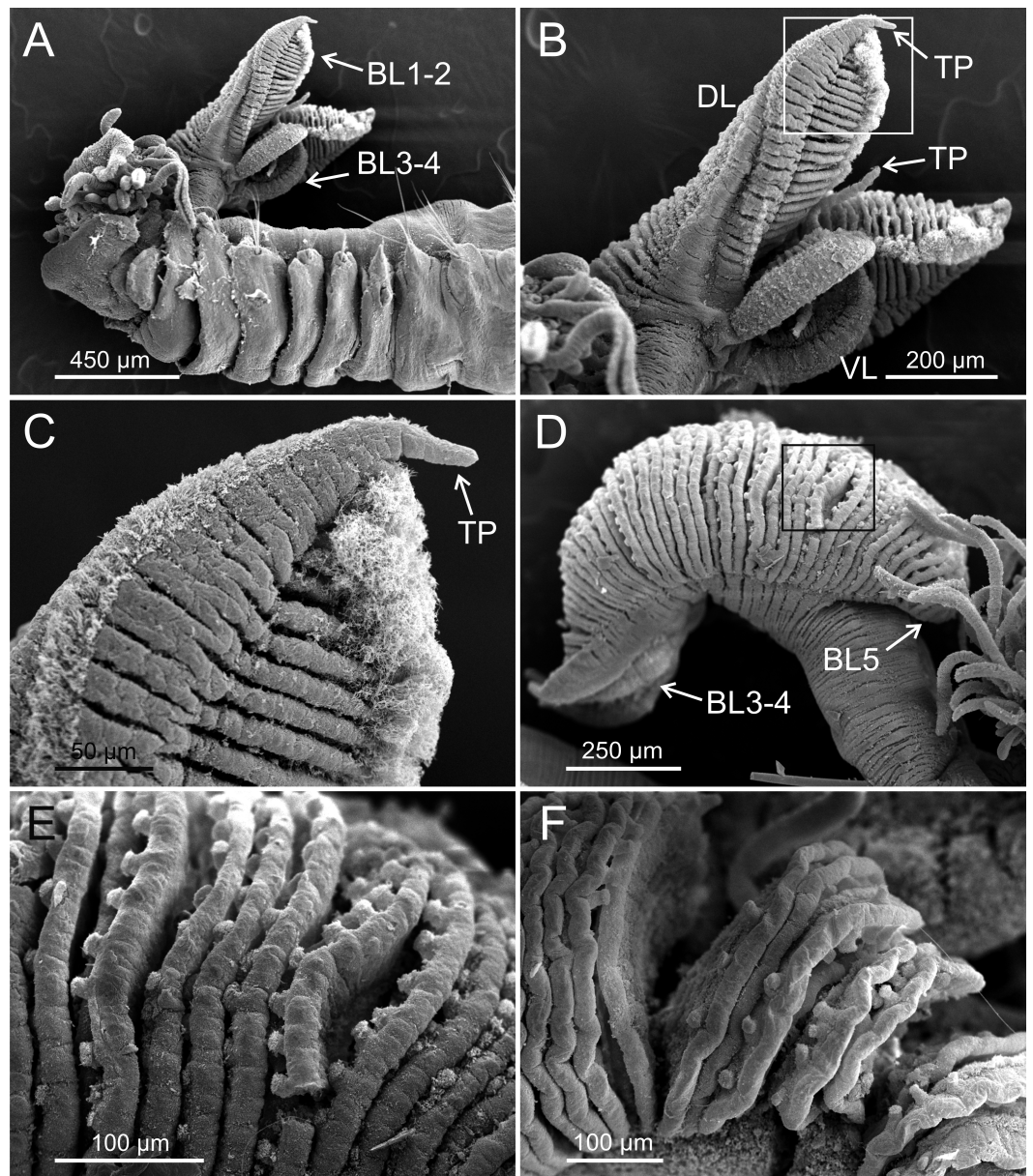


Figure 3 SEM micrographs of paratypes of *Terebellides hutchingsae* spec. nov. from Thailand. *Terebellides hutchingsae* spec. nov., SEM micrographs of paratypes, MNCN 16.01/17439 and MNCN 16.01/17436. (A) anterior end, left lateral view, showing lateral lappets and relative size of branchial lobes (BL); (B) detail of branchial lobes showing degree of fusion between dorsal (DL) and ventral (VL) lobes, framed area showed in (C); (C) detail of distal end of left dorsal lobe showing ciliary fields and terminal projection (TP); (D) right lateral view of branchiae, framed area showed in (E); (E-F) detail of ciliated papillae of branchial lobes lamellae.

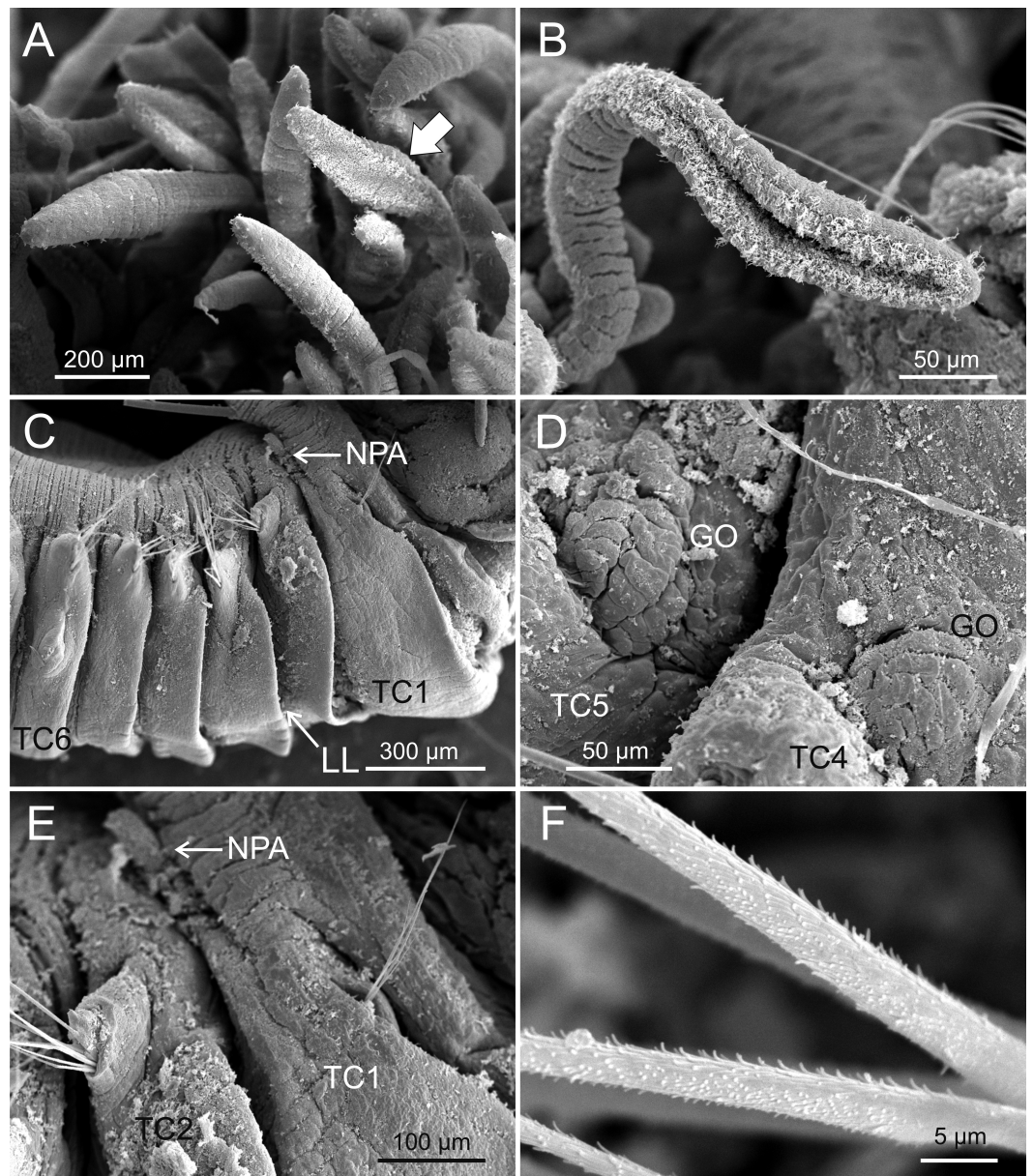


Figure 4 SEM micrographs of paratypes from Thailand and Myanmar. *Terebellides hutchingsae* spec. nov., SEM micrographs of paratypes, MNCN 16.01/17432 and MNCN 16.01/17454. (A) several buccal tentacles, one showing ciliated side of distal end (arrowhead); (B) detail of ciliated distal end of a buccal tentacle; (C) anterior end, left lateral view, showing lateral lappets (LL) from thoracic chaetiger 1 (TC1) to thoracic chaetiger 6 (TC6) and nephridial papilla (NPA) in thoracic chaetiger 1; (D) detail of genital opening (GO) of thoracic chaetiger 4 (TC4) and thoracic chaetiger 5 (TC5); (E) thoracic chaetiger 1 (TC1) and thoracic chaetiger 2 (TC2) notopodia showing reduction of TC1; (F) detail of pilose surface of thoracic notochaetae.

Lateral lappets on TC1–5 (SGIII–VII), being larger in TC1–3 (Figs. 2B, 3A, 4C and 6A). No conspicuous dorsal rounded projection on anterior chaetigers or oval-shaped glandular region in TC3. Both notopodia and notochaetae in TC1 less developed than in following chaetigers (Figs. 3A, 4C and 4E).

Branchiae arising as single structure from SGII–III, with a single, mid-dorsal, stalk and two pairs of unfused lobes; lower (=ventral) (BL3–4) pair smaller and much shorter than upper (=dorsal) (BL1–2) pair of lobes (Figs. 3A–3B and 6B–6C). Upper and lower lobes with a short terminal pointed projection (although deciduous and sometimes damaged) (Fig. 3C). Dorsal pair of branchial lobes with short anterior projection (fifth lobe; BL5) (Fig. 3D), sometimes hidden behind buccal tentacles (Figs. 2A and 2B). Loss of any of branchial lobes not observed. One side of branchial lamellae with parallel bent rows of cilia and well-developed ciliated papillae on edge of one side of each branchial lamella (Figs. 3D–3F).

Eighteen thoracic chaetigers (SGIII–XX), all with notopodia; neuropodia from SGVIII. Notopodia of TC1 smaller than following ones (Figs. 4C and 4E); all remaining notopodia similar in size. Thoracic neuropodia as sessile pinnules, from TC6 (SGVIII) to TC18 (SGXX), with uncini in single rows from TC7 (SGIX) throughout. Thoracic notochaetae similar in length, with textured surface (Fig. 4F). Ciliated papilla dorsal to each thoracic notopodia not observed. First thoracic neuropodia (TC6) with 4–7 geniculate acicular chaetae with minute teeth in their upper part forming a *capitulum* easily overlooked without SEM (Figs. 6E–6F); sharply bend. Subsequent thoracic neuropodia with one row of about 8–10 uncini per torus (Fig. 5A); uncini as shafted denticulate hooks with long, pointed *rostrum* surmounted by 4–5 teeth and an upper crest of several smaller denticles of different sizes (Figs. 5A–5C). One finger-shaped nephridial papilla basal to branchial stem (Fig. 4E); genital openings, dorsal to notopodia in TC4 and TC5 (Figs. 4D and 6D).

Twenty seven to 30 abdominal chaetigers (30 in holotype). Abdominal neuropodia as erect pinnules, with about 30 uncini per torus (Fig. 5D). Uncini with 3–4 teeth above *rostrum* (Figs. 5E and 5F), surmounted by a row of an irregular number of shorter teeth and an upper crest of minute teeth. Pygidium blunt, funnel-like depression. No eggs were observed in body cavity of holotype, but mature females of smaller size were observed (9.0 mm length, 1.0 mm width). Colour in alcohol pale brown.

Methyl green staining resembling pattern 1 of Schüller & Hutchings (2010), resulting in a solid green coloration from CH1 to CH9, then turning into striped pattern from CH10 to CH12 and fading in following segments. Additional pronounced staining also on short ventral branchial lobes (BL3–4) and postero-ventral part of branchial upper lobes (BL1–2).

Type locality

Gulf of Thailand, muddy bottom at 66 m depth.

Distribution and habitat

Specimens of *T. hutchingsae* **spec. nov.** were found in shallow water bottoms (45.5–51.0 m depth) about 80 km off the coast of Myanmar (North Andaman Sea) and in slight deeper bottoms (61.0–78.0 m depth) in the outer end of the Gulf of Thailand (Table 1 and Fig. 7). Sediments are typically muddy with high values of organic carbon (0.74–2.42%) and of silt and clay fraction (69.6%–95.4%).

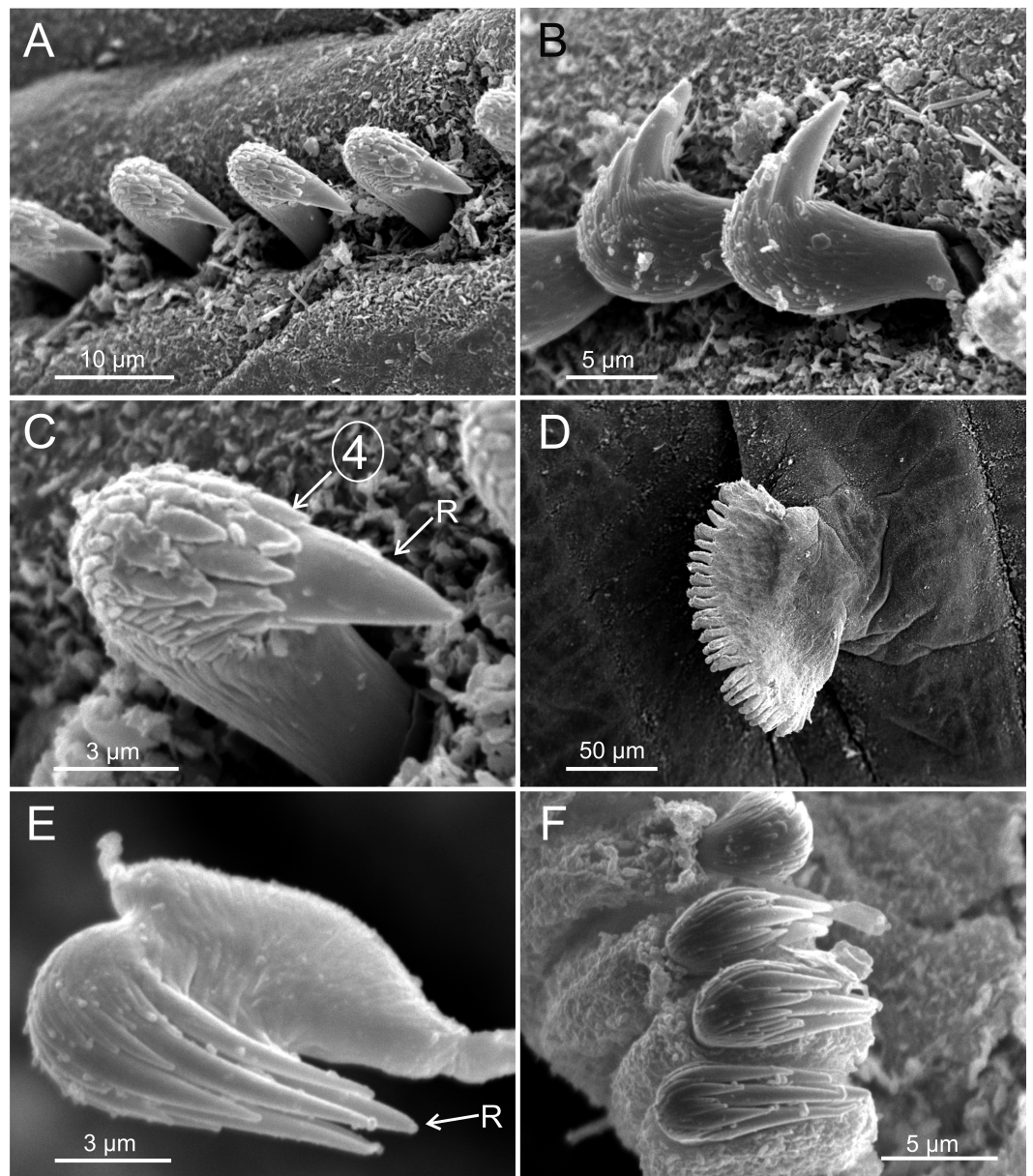


Figure 5 SEM micrographs of paratypes from Thailand and Myanmar, Cont. *Terebellides hutchingsae* spec. nov., SEM micrographs of paratypes, MNCN 16.01/17432 and MNCN 16.01/17454. (A) row of uncini in a thoracic uncinigerous torus in latero-frontal view; (B) detail of two thoracic uncini in lateral view; (C) detail of a thoracic uncinus in frontal view showing *rostrum* (R) and four teeth forming first row of *capitulum* denticles; (D) one abdominal neuropodial pinnule; (E) one abdominal uncinus in upper view showing first row of *capitulum* denticles almost reaching tip of *rostrum* (R); (F) four abdominal uncini in upper view.

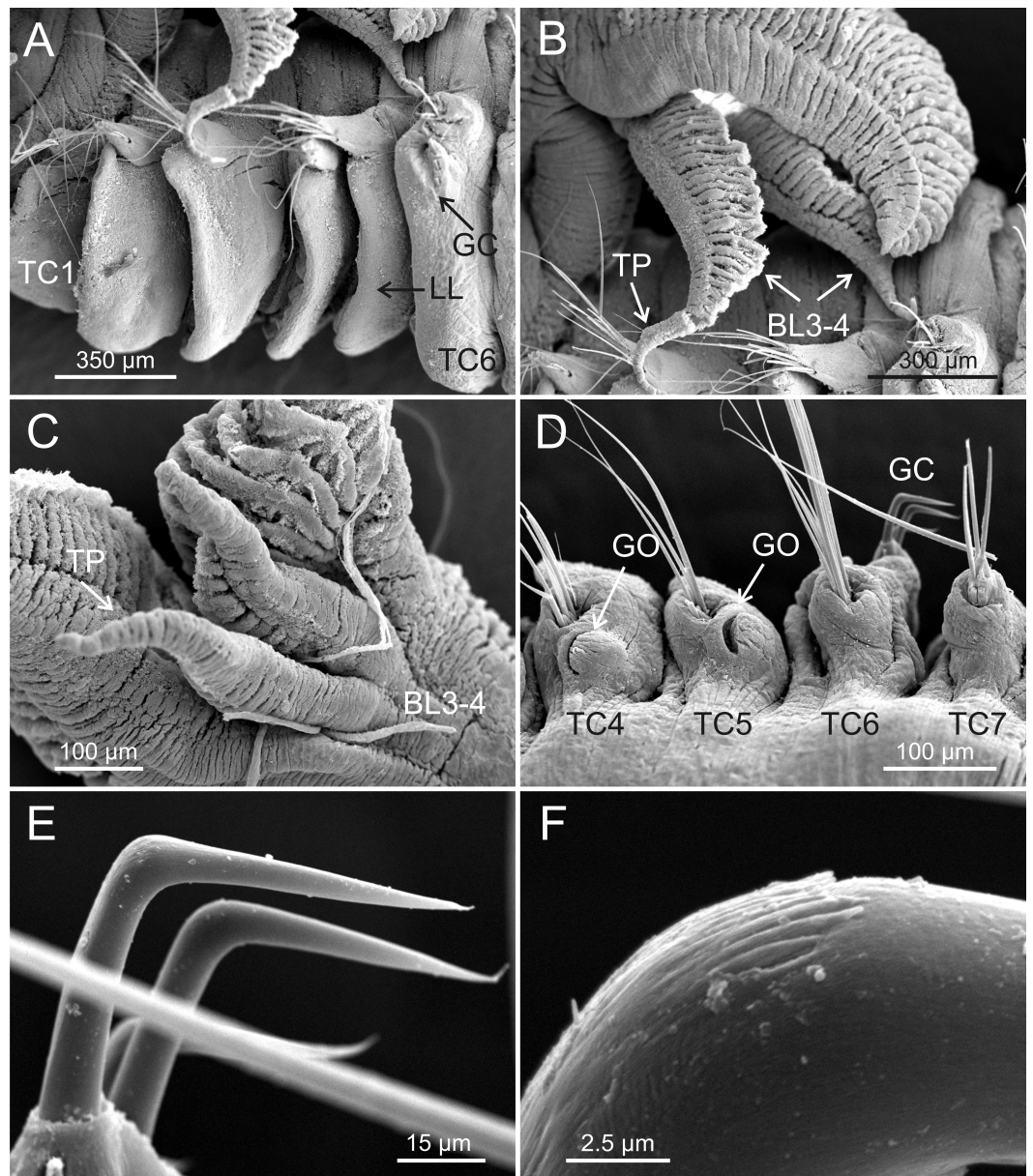


Figure 6 SEM micrographs of paratypes from Myanmar. *Terebellides hutchingsae* spec. nov., SEM micrographs of paratypes, MNCN 16.01/17451 and MNCN 16.01/17454. (A) anterior end, left lateral view, showing lateral lappets (LL) from thoracic chaetiger 1 (TC1) to thoracic chaetiger 6 (TC6) and geniculate chaetae (GC) in thoracic chaetiger 6; (B) lateral view of lower branchial lobes (BL3–4) showing terminal projection (TP); (C) ventral view of lower branchial lobes (BL3–4) with terminal projection (TP); (D) dorsal view of thoracic chaetiger 4 (TC4) to thoracic chaetiger 7 (TC7) showing genital openings (GO) at TC4 and TC5, and geniculate chaetae (GC) at TC6 and TC7; (E) thoracic chaetiger 6 geniculate chaetae in lateral view; (F) detail of *capitium* of one geniculate chaeta.

Etymology

The species is named after Dr. Pat Hutchings, for her many contributions to the taxonomy of Terebelliform polychaetes in Australia and SW Pacific waters, and particularly to the genus *Terebellides*, and also for her key role in the study of Australian polychaetes.

***Terebellides* cf. *woolawa* Hutchings & Peart, 2000**

(Figs. 2C–2D and 7)

Material examined

MNCN 16.01/17455 (St. S4(3), 1 spec.); MNCN 16.01/17456 (St. WP3(3), 1 spec.).

Distribution and habitat

Both specimens of *T. cf. woolawa* were found in two shallow water stations (51.0 m depth) about 80 km off the mouth of the Irawadi river in the coast of Myanmar (North Andaman Sea) (Table 1).

***Terebellides* sp.**

(Figs. 1B, 2E–2F and 7)

Material examined

MNCN 16.01/17457 (St. S4(3), 1 spec.).

Distribution and habitat

The specimen was found in a shallow water bottom (51 m depth) about 16 km off the coast of Myanmar (North Andaman Sea) (Table 1).

Key of SE Indo-Pacific species of *Terebellides*

The key here presented has been modified from a previous key of Australian Trichobranchidae by Hutchings & Peart (2000), which was based on a limited number of easy-to-detect characters: (1) number of chaetigers with geniculate chaetae, (2) degree of development of thoracic notopodia, and (3) shape of branchiae, giving special emphasis to the relative size of branchial lobes. *Terebellides ypsilon* Grube, 1878, from the Philippines, was not included because the description is very brief and following Hutchings & Peart (2000), who revised the type material, the taxon should be considered as undeterminable.

1. Geniculate chaetae in two thoracic chaetigers 2
 - Geniculate chaetae in one thoracic chaetiger 4
2. All thoracic notopodia of similar length 3
 - Thoracic notopodia from thoracic chaetiger 6 onwards much bigger and with more numerous and longer notochaetae *T. intoshi* Caullery, 1944
3. Thoracic uncinigers with geniculate chaetae similar in shape and position¹ *T. akares* Hutchings, Nogueira & Carrerette, 2015
 - Thoracic uncinigers with geniculate chaetae different in shape and position *Terebellides* sp.
4. Geniculate chaetae in thoracic chaetiger 7² *T. sieboldi* Kinberg, 1866
 - Geniculate chaetae in thoracic chaetiger 6 5

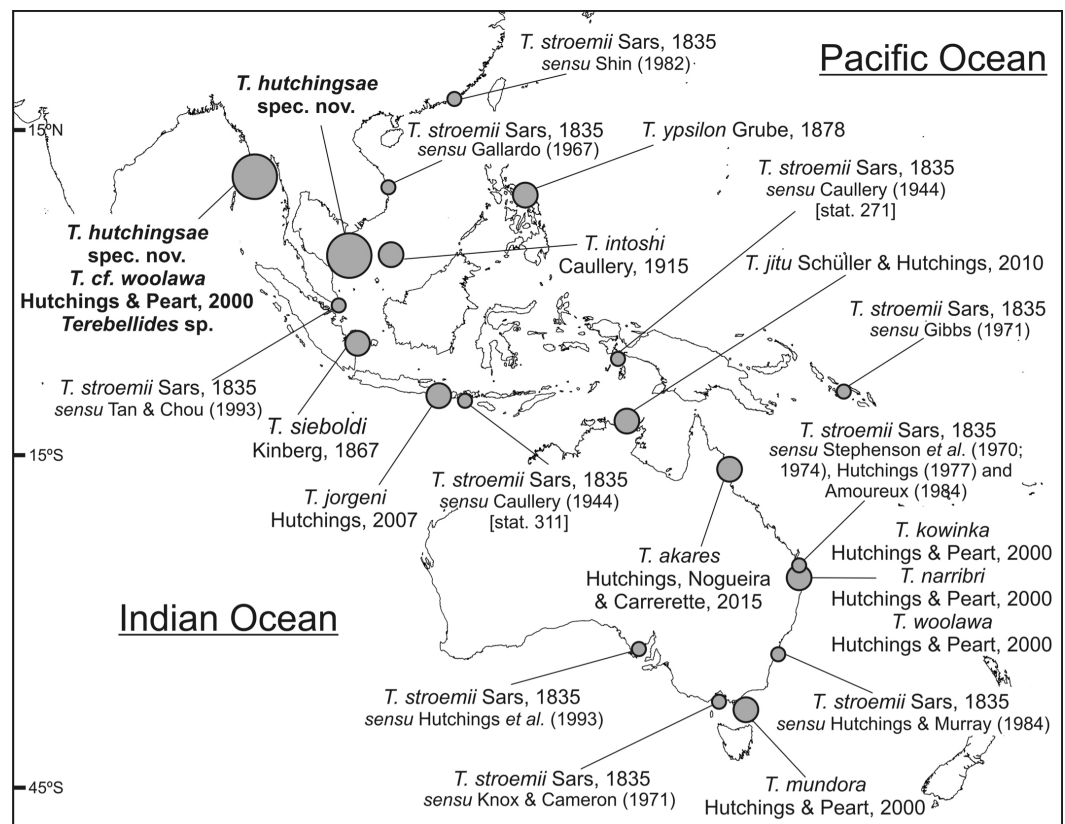


Figure 7 Map of SW Indo-Pacific Ocean. Map of SW Indo-Pacific Ocean showing locations where species of *Terebellides* reported in this paper were found (big circles), along with type localities of other *Terebellides* species previously described (medium circles) or reported (small circles).

5. Branchial lobes 1–4 not fused *T. mundora* Hutchings & Peart, 2000
- Branchial lobes 1–4 more or less fused 6
6. Four branchial lobes 7
- Five branchial lobes 8
7. All thoracic notopodia similar in size and well developed *T. kowinka* Hutchings & Peart, 2000
- Thoracic notopodia 1 and 2 much smaller than subsequent ones *T. jorgeni* Hutchings, 2007
8. Branchial lobe 5 about 1/5 length of posterior lobes; thoracic lateral lappets without dorsal projections, geniculate chaetae of thoracic chaetiger 6 sharply bent 9
- Branchial lobe 5 almost 1/2 length of posterior lobes; lateral lappets of thoracic chaetigers 1–4 with dorsal projections, geniculate chaetae of thoracic chaetiger 6 gently curved *T. woolawa* Hutchings & Peart, 2000
9. Thoracic notopodia 1 not reduced; large, white, oval glandular patches in thoracic notopodia 3 *T. narribri* Hutchings & Peart, 2000
- Thoracic notopodia 1 strongly reduced; no glandular patches in thoracic notopodia 3 10

10. All branchial lobes of similar length and fused half of their length; branchial lamellae with transverse ridges of ciliature *T. jitu* Schüller & Hutchings, 2010

- Ventral (lower) branchial lobes much shorter than dorsal (upper) ones and fused basally; branchial lamellae with ciliated transverse ridges of ciliature and ciliated papillae *T. hutchingsae* spec. nov.

- (1) Those of first pair (segment 7) are shorter.
- (2) The position of GC in TC7 (SG9) is very unusual in the genus *Terebellides*; this feature is apparently only shared with *T. pacifica* Kinberg, 1866, a species which has been removed from synonymy with *T. stroemii* by Garraffoni, Lana & Hutchings (2005).

DISCUSSION

On *Terebellides hutchingsae* spec. nov.

Five species of *Terebellides* were previously described in the equatorial Indo-Pacific region (Fig. 7): *T. intoshi* Caullery, 1915, *T. sieboldi* Kinberg, 1866, *T. ypsilon* Grube, 1878, *T. jorgeni* Hutchings, 2007 and *T. jitu* Schüller & Hutchings, 2010. *Terebellides intoshi* is characterised by the large size of the notopodia and notochaetae from TC6 onwards (Fig. 8A) and probably by the presence of two chaetigers with geniculate chaetae as well (see also the discussion on *Terebellides* sp.); *T. sieboldi* has geniculate chaetae in TC7 (SG9) instead of TC6 and *T. ypsilon* is considered undeterminable by Hutchings & Peart (2000) because type material no longer exists. The two most recently described species, *Terebellides jorgeni* and *T. jitu*, are the most similar to *T. hutchingsae* spec. nov. The overall shape of branchiae is quite similar in *T. jorgeni* and *T. hutchingsae* sp. nov., being lobes 1–4 unequally sized and entirely free (not fused), with upper (dorsal) ones larger than lower (ventral) ones, and with “surface of branchial lamellae weakly papillate” (cfr. p. 78 in Hutchings, 2007); the latter probably refers to the presence of ciliated papillae, which is a feature difficult to confirm in the original figures. On the other hand, *T. jorgeni* differs from the new species in: (1) the presence of glandular and whitish ventral part of anterior segments, SG5 to SG9 (CH3 to CH7) but specially on SG5 to SG7 (absent in *T. hutchingsae* sp. nov.), and bearing pronounced thickening and elevation of dorsal anterior margins forming dorsal crests; (2) genital openings are present in SG4 and SG5, instead of SG6 and SG7 (TC4 and TC5) as in *T. hutchingsae* spec. nov.; (3) the branchiae are formed by four lobes instead of five.

According to the original description, *T. jitu* is also similar to *T. hutchingsae* spec. nov. but all branchial lobes are of similar length and have half of their length fused, instead of the lower ones being much shorter and fused basally as in *T. hutchingsae* spec. nov.

Terebellides narribri Hutchings & Peart, 2000 and *T. woolawa* Hutchings & Peart, 2000 were described from the NE Australian coast. Both species share with *T. hutchingsae* spec. nov. branchiae with similar shape and composed by five lobes; *T. narribri* differs from the new species by having first thoracic notopodia (TN1) of same size as the following, and TC3 bearing large, white, oval pair of glandular patches. *Terebellides woolawa* is characterised by the great development of BL5 (but see discussion on *T. cf. woolawa*) and by having anterior thoracic segments with dorsal projections on lateral lappets, which are absent in *T. hutchingsae* spec. nov.

Out of the Indo-Pacific area, there are no reports yet of any species gathering the same set of characters as *T. hutchingsae* **spec. nov.** However, seven more species have been described with branchial lamellae having ciliated papillae (Solís-Weiss, Fauchald & Blanckstein, 1991; Bremec & Elías, 1999; Parapar et al., 2016). These are *T. klemanni* Kinberg, 1867, *T. anguicomus* Müller, 1858, *T. carmenensis* Solís-Weiss, Fauchald & Blanckstein, 1991, *T. parvus* Solís-Weiss, Fauchald & Blanckstein, 1991, *T. lanai* Solís-Weiss, Fauchald & Blanckstein, 1991, *T. totae* Bremec & Elías, 1999 and *T. persiae* Parapar et al., 2016. Four of them differ from our new species in having “thoracic dorsal hump”: *T. anguicomus* (which also has 17 thoracic chaetigers instead of the 18 in *T. hutchingsae* **spec. nov.**), *T. carmenensis*, *T. totae* (which also has all four branchial lobes similar in length, while the ventral ones are much shorter in *T. hutchingsae* **spec. nov.**) and *T. persiae*. As for the three remaining species, *T. klemanni* has all branchial lobes of similar length and free almost to base, and gently curved geniculate acicular chaetae instead of being sharply bent, *T. lanai* has only one type of buccal tentacles, instead of two, and branchial lobes are fused in most of their length; and *T. parvus* is characterized by having a very low number of abdominal segments (20–26 instead of 27–30 in our new species).

Finally, two species show tufts of cilia at the edge of the branchial lamellae: *T. mediterranea* Parapar, Mikac & Fiege, 2013, and *T. gracilis* (Malm, 1874) both from Iceland, *sensu* Parapar, Moreira & Helgason (2011), and from the Adriatic sea, *sensu* Parapar, Mikac & Fiege (2013), but in these two species the cilia arise directly from the lamella surface and not from the tip of a papilla as in *T. hutchingsae* **spec. nov.**

On *Terebellides* cf. *woolawa* and *Terebellides* sp.

Terebellides woolawa is characterised by the well-developed fifth branchial lobe (BL5) and the presence of dorsal rounded projections on lateral lappets of SG 3–6 (TC1–4). This large species was described from intertidal to shallow water habitats in eastern Australia (Fig. 7) and was found across most of Australian coasts (Hutchings & Peart, 2000). Specimens found in this study are large-sized, and agree fairly well with the original description; in particular, specimen MNCN 16.01/17455 shows the typical shape of the branchiae, which have five lobes, BL1–4 are fused up to half of their length, filamentous tips are short, and BL5 is well developed (Figs. 2C and 2D). Nevertheless, our specimens lack the characteristic dorsal lobes of anterior thoracic lateral lappets: this prevented to fully confirm the identity of our material.

In turn, the specimen identified as *Terebellides* sp. differs from *T. hutchingsae* **spec. nov.** and *Terebellides* cf. *woolawa* in two features: (1) BL5 is large-sized, about half the length of posterior lobes (BL1–4); and (2) TC5 and TC6 are both provided with acicular geniculate chaetae. Thus, BL5 is longer than in any other described species including *T. woolawa*. However, this might be due to the preservation state of the specimen, which is slightly deteriorated. Anyway, the combination of the two aforementioned characters may justify the erection of a new species, but we prefer to wait for eventually finding additional specimens to confirm its status.

On the other hand, four species of *Terebellides* were previously described as having geniculate chaetae in two thoracic chaetigers. Two species are known from the French

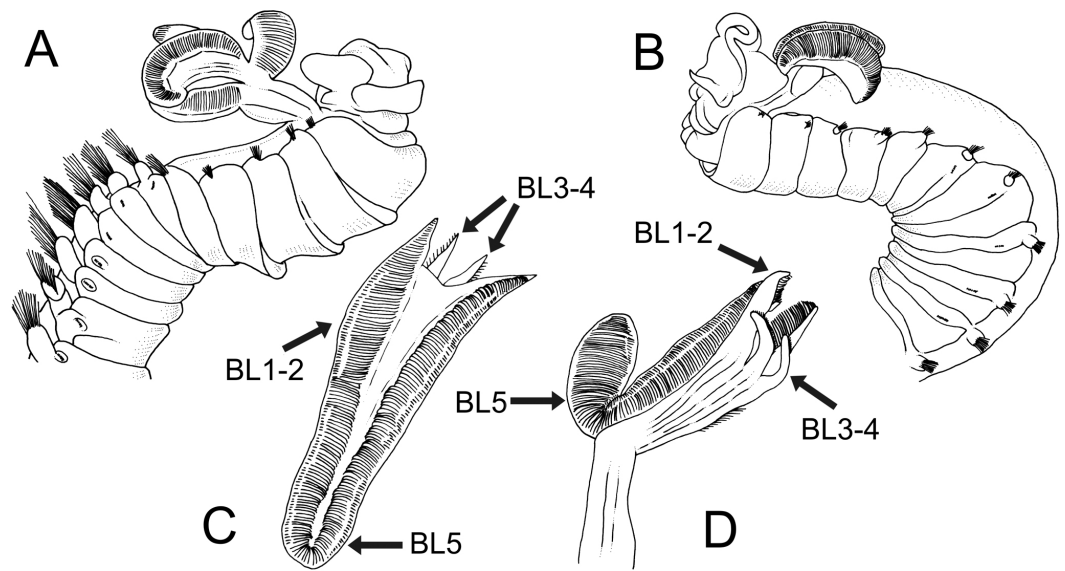


Figure 8 Line drawings of two *Terebellides* species previously described or reported in SW Pacific Ocean by Caullery (1915), redrawn from original. *Terebellides intoshi* Caullery, 1915; (A) anterior end in right lateral view showing great size of notopodia and notochaetae of thoracic chaetigers from thoracic chaetiger 6 onwards. *Terebellides stroemii* Sars, 1835; (B) anterior end in left lateral view; (C–D) dorsal and ventral view of branchial lobes showing high development of fifth branchial lobe (BL5), small size of branchial ventral lobes (BL3–BL4) and high degree of fusion of all posterior lobes (BL1–BL4).

Polynesia and Iceland: *T. biaciculata* Hartmann-Schröder, 1992 and *T. bigeniculatus* Parapar, Moreira & Helgason, 2011, respectively. The other two belong to the Indo-Pacific region: *T. akares* Hutchings, Nogueira & Carrerette, 2015 and *T. intoshi* Caullery, 1945 sensu Imajima & Williams (1985), from North-East Australia and Japan, respectively. We follow Parapar, Moreira & Helgason (2011) in considering that type material of *T. intoshi* from South China Sea probably does not have two chaetigers with geniculate chaetae. Thus, the Japanese material would belong to a different species. Anyway, they differ from *Terebellides* sp. in the branchial shape and the greater development of thoracic notopodia from TC6 (Fig. 8A). In turn, *T. akares*, have branchiae bearing a much shorter BL5 and the posterior ventral lobes (BL3–4) are completely free from each other, contrary to *Terebellides* sp., in which these lobes are fused in most of their length (Fig. 2F). The observed differences between these Indo-Pacific species and *Terebellides* sp. reinforce its status as new species, so that further efforts should be addressed to find new materials allowing to formally describe it.

On *Terebellides stroemii* in Indo-Pacific waters

The North Atlantic species and type species of the genus *Terebellides*, *T. stroemii* Sars, 1835, was also widely reported in the Indo-Pacific area. For instance, in Indonesia by Caullery (1944), in South Korea by Gallardo (1967), in Hong Kong by Shin (1982), in Singapore by Tan & Chou (1993) and in the Australian coasts by Stephenson, Williams & Lance (1970), Stephenson, Williams & Cook (1974), Knox & Cameron (1971), Hutchings (1977), Amoureux (1984), Hutchings & Murray (1984) and Hutchings et al. (1993) (Fig. 7). In the

Southern Pacific Ocean, the presence of *T. stroemii* was denied by [Hutchings & Peart \(2000\)](#) after examining Norwegian material. Indeed, these authors already reassigned part of these Indo-Pacific reports to other species, while others specimens were not. Among them, the material reported by [Caullery \(1944\)](#) and collected during the Siboga expedition might well correspond to more than one species according to the description and illustrations. The shape of the branchiae in specimen from station 271 (Fig. 147 in [Caullery, 1944](#); redrawn here in [Fig. 8B](#)) and station 311 (Fig. 148 in [Caullery, 1944](#); redrawn here in [Figs. 8C and 8D](#)) sharply differs in BL5 size; the specimen of station 311 is more similar in branchial shape to *T. hutchingsae* **spec. nov.** but differs in the high degree of fusion of dorsal and ventral lobes in Caullery's material (see [Fig. 8D](#)). The specimen reported by [Gallardo \(1967\)](#) cannot be properly identified because the description is quite brief (e.g., "The branchia has the typical shape...") and only a lateral view of a thoracic uncinus is illustrated and this is not relevant in species discrimination. More recently, [Parapar & Hutchings \(2015\)](#) redescribed *T. stroemii* based on Norwegian specimens collected by Michael Sars near the type locality. Therefore, the type species is now well-illustrated based on the most recent, taxonomically robust characters. This redescription, together with the previous observations and our present results, certainly allows us to strongly support the absence of *T. stroemii* from Indo-Pacific waters.

Taxonomic relevance of the ciliated papillae of branchial lamellae

One of the most relevant diagnostic characters of *T. hutchingsae* **spec. nov.** is the presence of ciliated papillae in branchial lamellae. This character was long ignored in *Terebellides* descriptions and was discussed by [Parapar, Moreira & O'Reilly \(2016\)](#) and [Parapar et al. \(2016\)](#). In fact, several recently described species from across the world oceans show this feature ([Table 2](#)), namely *T. gracilis* [Malm, 1874 sensu Parapar, Moreira & Helgason \(2011\)](#), off Iceland; *T. jorgeni* [Hutchings, 2007](#), from Indonesia; *T. gracilis* [Malm, 1874 sensu Parapar, Mikac & Fiege \(2013\)](#) and *T. mediterranea* [Parapar, Mikac & Fiege, 2013](#), from the Adriatic Sea; *T. akares* [Hutchings, Nogueira & Carreterre, 2015](#), from the Great Barrier Reef (NE Australia); *T. persiae* [Parapar et al., 2016](#), from the Persian Gulf and *T. cf. woolawa* [Hutchings & Peart, 2000 sensu Parapar et al. \(this work\)](#) from South Myanmar. This character is probably much more widespread and shows at least two different morphotypes: (1) low papillae as it was found in *T. gracilis* from Iceland and the Mediterranean, and (2) well developed papillae in the rest of species. The presence of these low ciliated papillae reported in Icelandic and Adriatic specimens of *T. gracilis* by [Parapar, Moreira & Helgason \(2011\)](#) and [Parapar, Mikac & Fiege \(2013\)](#) was confirmed in the holotype. Therefore, these ciliated papillae appear as a robust taxonomic character and we strongly recommend taking it into account in future descriptions of new species within the genus.

Abbreviations used in text, tables and figures

BL	Branchial lobes
BT	Buccal tentacles
CHG	Chaetiger with geniculate chaetae
DL	Dorsal lobes

GC	Geniculate chaeta
GO	Genital opening
LL	Lateral lappets
NACH	Number of abdominal chaetigers
LCP	Low ciliated papillae
NPA	Nephridial papilla
NRTU	Number of rows of frontal rostral teeth in thoracic uncini
PPP	Posterior pointed projection
R	Rostrum
SG	Segment
TC	Thoracic chaetiger
TN	Thoracic notopodia
TP	Terminal projection
VL	Ventral lobes
WDCP	Well developed ciliated papillae

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Competing Interests

The authors declare there are no competing interests.

Author Contributions

- Julio Parapar and Juan Moreira performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Daniel Martin conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.

Data Availability

The following information was supplied regarding data availability:

The raw data is contained in [Table 1](#).

New Species Registration

The following information was supplied regarding the registration of a newly described species:

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Terebellides hutchingsae species LSID: urn:lsid:zoobank.org:act:78E96984-41E7-43E6-8E5D-03E9421BE306.

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